

The aberrant inflorescence of *Luzula elegans* Lowe (Juncaceae) compared to other *Luzula* species

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Abstract:

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The aberrant inflorescence of *Luzula elegans* Lowe, the only annual species of the genus, is described. It differs strongly from all other inflorescence types found in *Luzula* L. However, each of the traditionally recognized subgenera (*Pterodes* Griseb., *Anthelaea* Griseb., *Luzula* (= *Gymnodes* Griseb.)) has an inflorescence type of its own. The results support the separation of *Luzula elegans* as an additional subgenus *Marlenia* as firstly proposed by EBINGER (1963). Subgenus *Pterodes* has the most ancestral inflorescence type, while in the subgenera *Anthelaea*, *Luzula* and *Marlenia* different derived stages are found.

Zusammenfassung:

Die Infloreszenz von *Luzula elegans* Lowe wird beschrieben. Sie weicht von allen sonst in der Gattung bekannten Blütenständen stark ab. Jedes der traditionell unterschiedenen Subgenera (*Pterodes*, *Anthelaea*, *Luzula* (= *Gymnodes*)) hat seinen eigenen Infloreszenztyp. Die vorliegenden Ergebnisse unterstützen den Vorschlag von EBINGER (1963), für *Luzula elegans* eine eigene Untergattung *Marlenia* einzuführen.

Introduction

Luzula elegans Lowe has a quite isolated position within the genus *Luzula*. CHRTEK & KRÍSA (1974) even described it as a separate genus *Ebingeria*. The name *Ebingeria* refers to a detailed study published by EBINGER (1963). He pronounced the differences between *L. elegans* and the remaining species of the subgenus *Anthelaea*, in which *L. elegans* was traditionally integrated since BUCHENAU (1865, 1906). Due to a number of morphological, anatomical and cytological differences, EBINGER proposed a subgenus *Marlenia*, consisting of *L. elegans* only. The isolated position of *L. elegans* is also pronounced by the fact that it is the only annual species in the genus.

Among the unique features of *L. elegans* is the inflorescence structure. Supplementary to the recently published analysis of the inflorescences of the Juncaceae (KÖBELE & TILLICH 2001), the present study adds an analysis of the aberrant inflorescence of *Luzula elegans* and aims to give an extended overview of the inflorescence types in *Luzula*.

The earliest investigation of the inflorescences of the Juncaceae was published by BUCHENAU (1865). He considers *L. elegans* (named *L. purpurea* L. de Buch) being a member of

subgenus *Anthelaea*, but emphasizes the unique character of its inflorescence. A more detailed study of the inflorescence structure was given by EBINGER (1963). Unfortunately, his terminology is somewhat unclear, and this makes it difficult to find unequivocal homologies to the inflorescences of the remaining *Luzula* species.

Results and discussion

The inflorescence of *L. elegans* superficially resembles those of subgenus *Pterodes* rather than subgenus *Anthelaea*, i.e. a single flower embraced by two bracts is found at the end of long internodes, thus the compound inflorescence has a loose habitus (figs. 1a, 2). As was recently shown for Juncaceae, the single flower with two bracts at its base represents a one-flowered spikelet. The flower originates from the axil of the lower bract and takes a pseudoterminal position. The upper bract is sterile (KÖBELE & TILLICH 2001).

It is characteristic for most species of *Juncus* and *Luzula*, that the paraclades overtop the axis from which they originate. This behaviour gives rise to the typical anthelodium. However, the relative main axis usually remains in a straight position when overtopped by lateral branches (fig. 1b). On the other hand, in *L. elegans* the main shoot is bent sideways in a more or less right angle by the lowermost paraclade, which itself continues the upright direction of the axis below and thus forms a sympodial continuation of the branching system. This behaviour is repeated by the paraclades of the next orders. Thus the complete inflorescence has an apparently straight and homogeneous main axis, which indeed is a monochasium (figs. 1a, 2, 4b). EBINGER (1963) calls this monochasial axis a pseudorachis.

At the (bended) main axis also the second paraclade of first order can repeat the behaviour of the first one, so that a double-bended main axis results (fig. 1a).

This unique inflorescence of *L. elegans* differs strongly from that of the three traditionally recognized subgenera of *Luzula*. Following Ebinger (1963), a fourth subgenus *Marlenia*, consisting of *L. elegans* only, should be added:

- Subgen. *Pterodes*,
- Subgen. *Anthelaea*,
- Subgen. *Luzula* sensu Ebinger 1963 (=Subgen. *Gymnodes* of BUCHENAU 1906),
- Subgen. *Marlenia*.

Each subgenus is characterized by its own typical inflorescence type (fig. 4). This may serve as an additional important argument for the natural circumscription of the subgenera. As can be seen from table 1, subgenus *Marlenia* is the most outstanding taxon in *Luzula*. The remaining subgenera are characterized essentially by inflorescence and seed characters.

All inflorescence types recognised so far in *Luzula* can be arranged in a morphological sequence. The probably ancestral inflorescence is found in subgenus *Pterodes*. Here the one-flowered spikelets (florescences) are separated by long internodes, the inflorescence has a very loose appearance (figs. 1b, 3a, 4a). The very same inflorescence structure is developed in *Juncus* L. sect. *Steirochloa* Griseb. (syn. subgen. *Poiophylli* Buchenau, see KIRSCHNER et al. 1999), as was recently described by KÖBELE & TILLICH (2001). It is noteworthy that *Juncus* sect. *Steirochloa* is closest to *Luzula* also with respect to anatomical characters (CUTLER 1969).

In subgenus *Anthelaea* only the proximal internodes of paraclades of lower orders are elongated, but then several paraclades of higher orders develop rather short internodes and gather to a more or less dense group at the distal part of lower order paraclades (figs. 3c, 4c). Finally, in subgenus *Luzula* the paraclades are differentiated into two clearly different types, the so-called short paraclades and long paraclades (TROLL 1965, S. 99). The short paraclades

bear only a basal prophyll, a very short epipodial internode and the one-flowered coflorescence. Several of these short praclades are grouped together at the distal end of the main axis to form a „spike“ of higher order, a complex pseudo-florescence. Below this distal agglomeration the synflorescence bears the long paraclades, which repeat the behaviour of the main axis (fig. 3d, 4d). Correlated to the differentiation into these two types of paraclades is a strong tendency of a truncation of the synflorescence, i.e. the loss of the distal spikelet (main florescence). Also the distal spikelet (coflorescence) of long paraclades often fails to develop (fig. 4d). This phenomenon is found in several families with polytelic synflorescences (WEBERLING & TROLL 1998), and it must be recognized as an far advanced character state. The aberrant inflorescence of subgenus *Marlenia* represents a much derived state of its own.

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Table 1: Selected character states of the subgenera of *Luzula*, from data of BUCHENAU (1906), MALHEIROS et. al. (1947), NORDENSKJÖLD (1949), EBINGER (1963), and own observations.

character	subgenus <i>Pterodes</i>	subgenus <i>Marlenia</i>	subgenus <i>Anthelaea</i>	subgenus <i>Luzula</i>
inflorescence	much branched anthelodium; all florescences long pedicelled	monochasial main axis, composed of successive first paraclades of increasing order	much branched anthelodium; florescences of higher order shortly pedicelled and crowded	often truncate synflorescence; with distal, crowded short paraclades and proximal long paraclades
seed	conspicuous chalazal (distal) caruncula	no caruncula, but very thick mucilaginous cover	caruncula missing or micropylar (basal), but very small	caruncula micropylar (basal), conspicuous
life span	perennial	annual	perennial	perennial
chromosomes	n = 6; < 2 μ m	n = 3; 4 – 6 μ m	n = 6; < 2 μ m	n = 6; < 2 μ m
leaf epidermis cells	ca. 40 \times 110 μ m anticlinal walls wavy	ca. 70 \times 280 μ m anticlinal walls smooth	ca. 40 \times 110 μ m anticlinal walls wavy	ca. 40 \times 110 μ m anticlinal walls wavy
stomata	ca. 40 μ m long	ca. 100 μ m long	ca. 40 μ m long	ca. 40 μ m long
mechanical tissue at leaf margin	present	absent	present	present
root endodermis cells	U-shaped	O-shaped	U-shaped	U-shaped

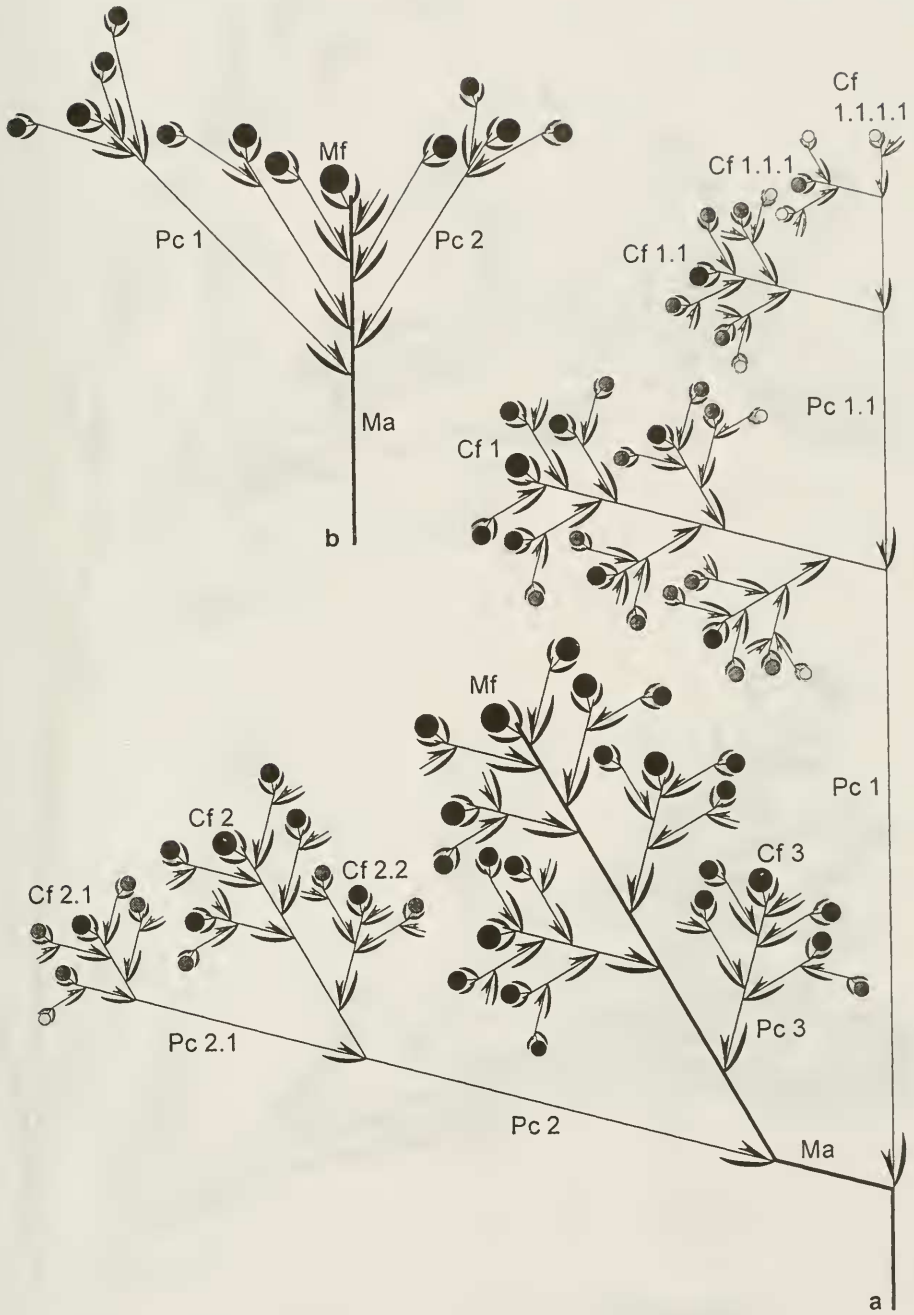


Fig. 1: *Luzula*. Schematic elevations of inflorescences. a: *L. elegans*; b: *L. pilosa*. Cf1, Cf2, Cf3: co-florescences of praclades of 1st order (originating from the main axis); Ma: main axis; Mf: main florescence; Pc1, Pc2, Pc3: consecutive praclades of 1st order; Pc1.1, Pc1.1.1, Pc1.1.1.1: praclades of increasing higher order;

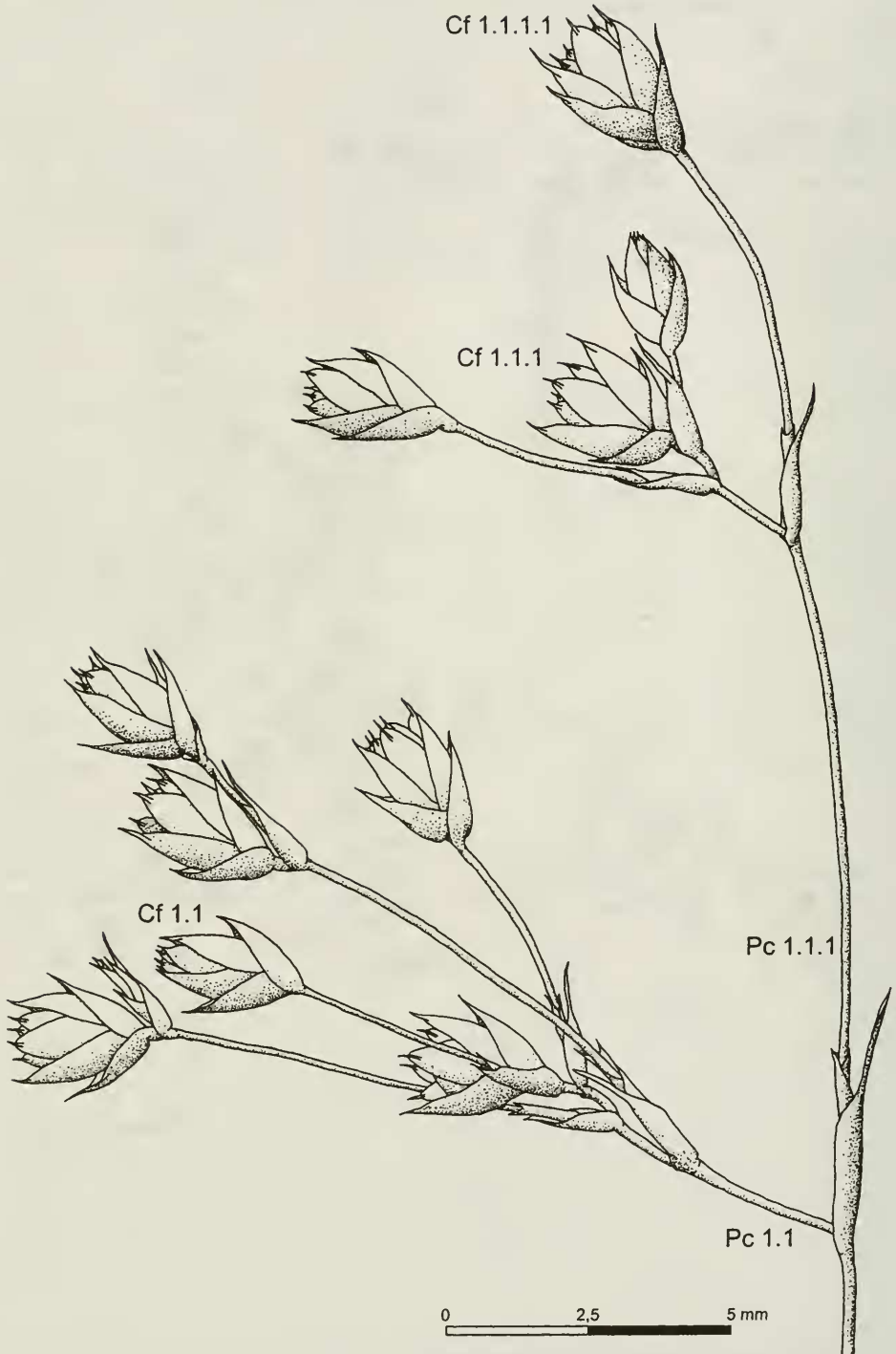


Fig. 2: *Luzula elegans*. Distal part of the inflorescence shown in fig. 1a. Abbreviations as in fig. 1.

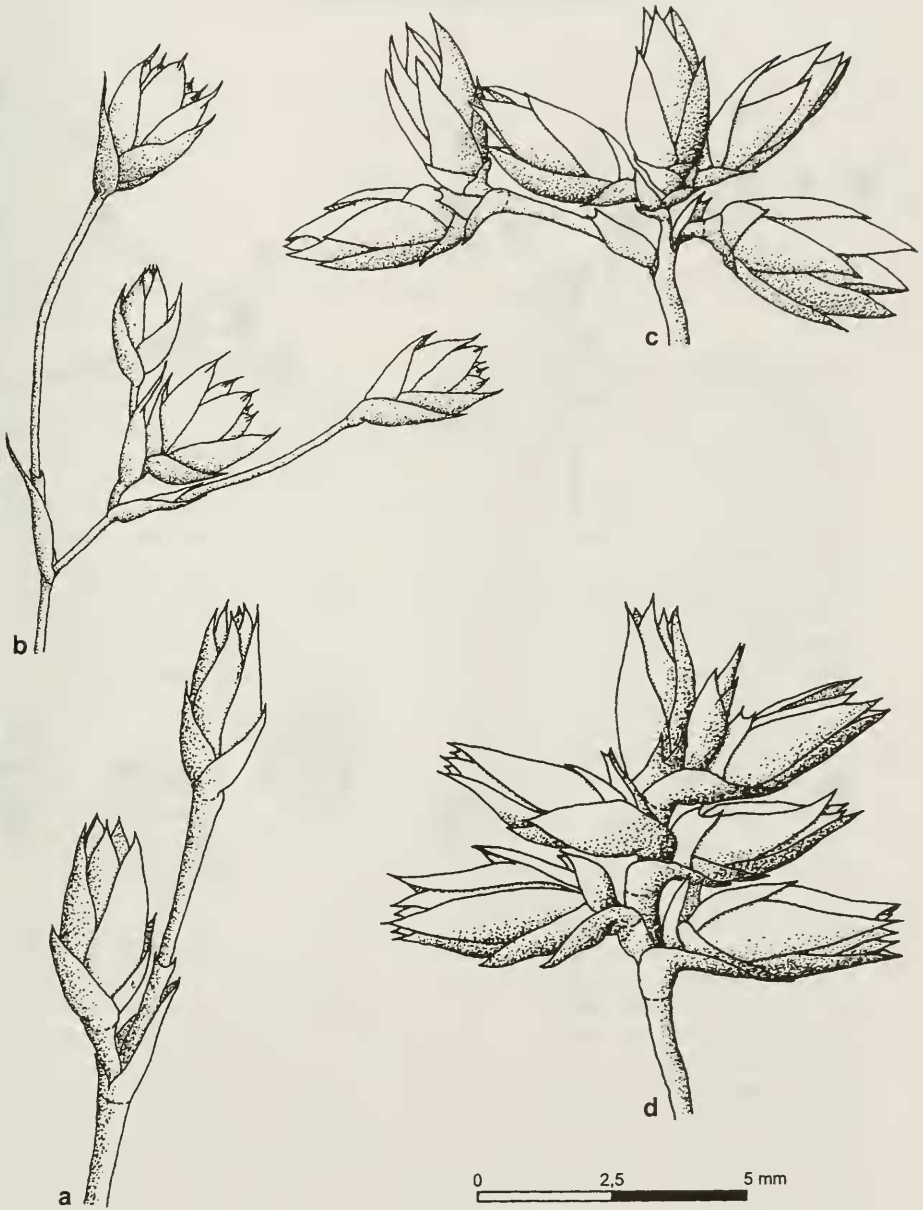


Fig. 3: Partial inflorescences of *Luzula*. a: *L. elegans* (subgen. *Marlenia*); b: *L. luzuloides* (subgen. *Anthelaea*); c: *L. pilosa* (subgen. *Pterodes*); d: *L. campestris* (subgen. *Luzula*).



Fig. 4: Diagrammatic comparison of the inflorescences of the subgenera of *Luzula*. a: subgen. *Pterodes*; b: subgen. *Marlenia*; c: subgen. *Anthelaea*; d: subgen. *Luzula*. The squares represent one-flowered florescences. The prophylls are omitted to increase the clearness. Note the tendency of truncation at the main axis and the long-paraclades in subgen. *Luzula*.